

## COMPARATIVE ECOLOGY OF TWO LINYPHIID SPIDERS (ARANEAE, LINYPHIIDAE)

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### ABSTRACT

*Frontinella pyramitela*, the Bowl and Doily Spider, and *Neriene radiata*, the Filmy Dome Spider, were the two most common linyphiid species in a study of sheetweb weaving and orbweaving guilds in central New Jersey. They differ in size when adult and in the relationship between prey size and spider size, but not in the absolute size of prey taken nor in their tendency to move from websites. Competition for websites is a negligible factor in the system, although the populations may be food-limited. These results are compared with studies by Wise (1975) and Riechert (1976, 1978, 1981).

### INTRODUCTION

In the course of a study on the foraging behavior of orbweavers (Araneidae) and sheetweb weavers (Linyphiidae) in central New Jersey (Janetos 1982), I marked numerous individuals of *Neriene radiata* (Walckenaer) and observed several characteristics of their foraging ecology. I also marked and observed another common linyphiid, *Frontinella pyramitela* (Walckenaer), the Bowl and Doily Spider. Here I report observations on both species and compare them to the experimental results of Wise's (1975) study on food limitation.

Both spiders were very common in the habitat in which I worked, and were the primary representatives of the family Linyphiidae. The space-filling webs of *F. pyramitela* and *N. radiata* occupy similar areas in the vegetation. The web of *F. pyramitela* consists of a sheet of silk pulled down into a bowl, with a flat sheet below that and a loose tangle of threads above. The spider runs upside-down on the bottom of the bowl. Small insects hit the loose tangle of threads and fall to the bowl, where the spider captures them from below. The web of *N. radiata* is a sheet of silk that has been pulled up into a dome, lacks a second sheet underneath, but has a loose silk tangle above. The spider runs upside-down under the dome and prey capture is similar to *F. pyramitela*. Thus, these species are ecologically and behaviorally similar in their foraging, i.e., they constitute a guild (Root 1967). I also report data gathered on the guild as an entity, to enable a comparison between the guild and its component species as well as to discover the source of variation in the guild's characteristics.

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## METHODS

The spiders were marked and censused in the course of a larger field study (Janetos 1982). The study site was the Stony Ford field station in Princeton, NJ, in old fields that were being re-invaded by various shrub and tree species. There was considerable floristic and structural diversity in the study area, but no closed canopy. I marked spiders in their webs by applying a small dot of model airplane paint. Websites were marked by tying a numbered strip of flagging tape onto the vegetation supporting the web. Spiders occasionally ran into the tangled threads or nearby vegetation during marking, but their subsequent behavior did not differ from unmarked individuals. All measurements of spider length, web size and prey size were made with a small plastic millimeter ruler, so that there was a minimum of disturbance by me. Daily censuses were made of all websites marked during the study, whether currently occupied or not. Flying prey were sampled by sticky traps similar in design to those introduced by Eberhard (1977).

Most of the data exhibit non-normal distributions. Statistical tests were thus non-parametric (Siegel 1956).

## RESULTS

Figure 1 shows the distributions of body lengths for each species. *Neriene radiata* is the larger of the two (*N. radiata*  $\bar{x}$  = 4.8 mm vs. *F. pyramitela*  $\bar{x}$  = 3.3 mm,  $p < 0.0001$ , Mann-Whitney U test). Interestingly, the coefficients of variation of the two distributions are similar (C. V. = 0.23 for *F. pyramitela* and C. V. = 0.15 for *N. radiata*). The variation in size within the guild is mainly due to the difference in average size between *F. pyramitela* and *N. radiata*. The low extreme of the size range is composed entirely of Bowl and Doily Spiders, while the high extreme is composed only of Filmy Dome Spiders. Only in the central part of the size range of the guild is there overlap between the two species.

The sheetweb weavers take more small size classes of flying prey than sampled by sticky traps (Fig. 2;  $\chi^2 = 11.5$ ,  $p < 0.05$ ). Uetz and Biere (1980) argue that such traps are biased in the direction of over-representing large prey. Thus, the linyphiids may take prey as a nearly random sample of their true availability.

The correlation between average prey size and spider size (Fig. 3) is slightly different for the two species. *N. radiata* exhibits very little influence of size on the average size of its prey ( $r_s = 0.049$ ), whereas the body length of *F. pyramitela* is strongly ( $r_s = 0.33$ ) and significantly ( $p < 0.01$ ) correlated with the average size of its prey. The guild as a whole shows strong positive correlations of spider size with average prey size in both field seasons (Fig. 4ab) (1978:  $r_s = 0.227$ ,  $p = 0.018$ ; 1979:  $r_s = 0.393$ ,  $p < 0.0001$ ).

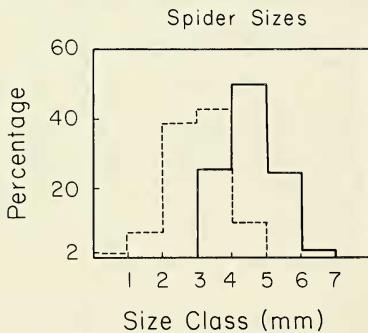


Fig. 1.—Histogram of body lengths of each species. Dashed line: *Frontinella pyramitela*,  $\bar{x}$  = 3.3 mm, N = 162. Solid line: *Neriene radiata*,  $\bar{x}$  = 4.8 mm, N = 59.

The distributions of residence time at a website for each species appear in Fig. 5. They are similar, although there is a statistically non-significant difference in the mean residence times (5.4 days for *F. pyramitela* and 3.9 days for *N. radiata*). Figure 5 also compares the distributions of residence times of *F. pyramitela* and *N. radiata* with those expected from a hypothesis of random spider movements (Janetos 1982). The Filmy Dome Spider has almost the same distribution of residence times that one would expect if the spider left web sites randomly. The Bowl and Doily Spider does not quite show the expected distribution of residence times. Most of the difference comes at the shortest residence time (1 day) where more cases were observed than expected. However, the rest of the deviations from expectation offer no clue to any pattern of behavior in the spiders. This is in striking contrast to the orbweavers in the same habitat (Janetos 1982).

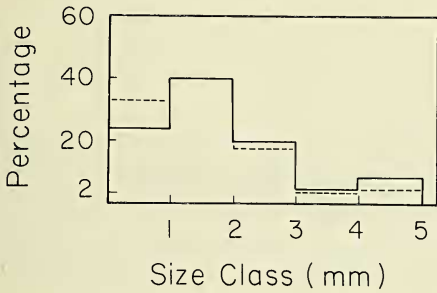


Fig. 2.—Distributions of body lengths of prey. Solid line: prey sampled by sticky traps, N = 332. Dashed line: prey observed in linyphiid webs in 1978 and 1979, N = 462. Distributions are significantly different,  $X^2_4 = 11.5$ ,  $p < 0.05$ .

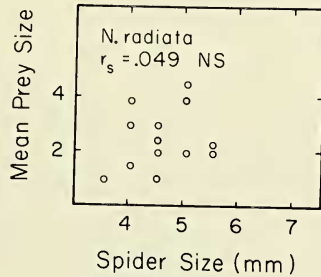
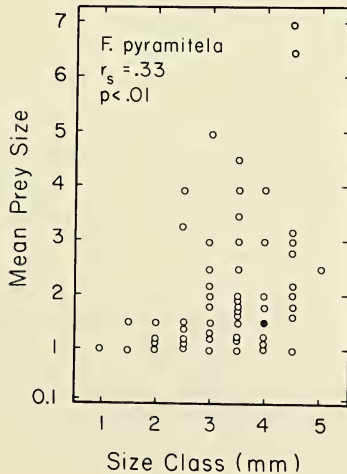


Fig. 3.—Average body length of prey in webs of each species of spider vs. body length of the spider. Upper graph: *Neriene radiata*. Lower graph: *Frontinella pyramitela*. Black dots indicate points where five or more observations overlap.



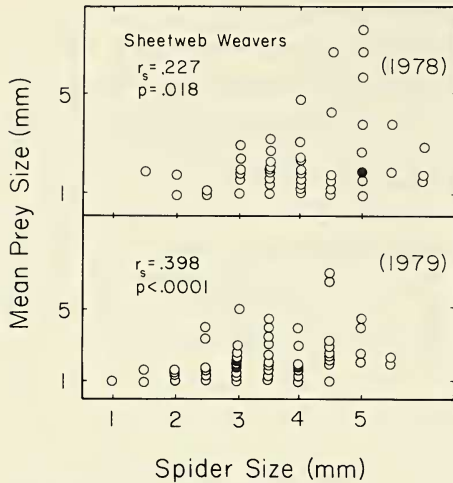


Fig. 4.—Average body length of prey in all webs of sheetweb weavers (pooled data) vs. body length of the spider. Upper graph; 1978 season. Lower graph: 1979. Black dots as in Fig. 3.

The sheetweb weaving guild showed no statistically significant relationship between body length and residence time at a website (Fig. 6) in either field season. Figure 7 shows the relationship for each species individually. Both species show similar rank correlation coefficients:  $r_s = -0.072$  for *N. radiata* and  $r_s = -0.079$  for *F. pyramitela*. These coefficients indicate that spider size contributes nothing to the variance in residence times for either species.

## DISCUSSION

The data in Figure 1 are cumulative. However, at any one time during the growing season, the pattern shown is representative: Filmy Dome and Bowl and Doily size ranges overlap a bit, with the former being on average larger than the latter.

The size of a predator is obviously important in determining its foraging tactics (Schoener 1969, Olive 1980, 1981ab). The predator's energy requirements, ability to overcome prey and capacity for locomotion all depend to some degree on its size. The relationship between the size of a predator and its prey should be fairly straight forward: large predators tend to take larger prey than do small predators (Schoener 1971, Werner and Hall 1974, Thompson 1975). However, large predators are usually also capable of taking prey from the small end of the size spectrum.

The difference in spider size has some effect on the size of prey captured by each species. Although the guild shows a strong correlation of spider size and prey size, the two species do not have the same relationship. The reason for this is subtle. The correlation between a predator's body size and the average body size of its prey should hold for those animals that must subdue their prey by force, or for those that are limited by the size of the apparatus by which they handle their prey. For poisonous animals, the relationship between predator size and prey size will be less clear (Enders 1976), but there is still a problem with delivering the poison. The prey must be snared by the web and subdued sufficiently so that the spider can approach and bite it without risk to itself. This requirement will limit the size of prey which small spiders can handle. Thus, one could predict that the correlation between predator size and prey size should be weaker for large predators. This prediction is upheld in the case of *F. pyramitela* and *N. radiata*.



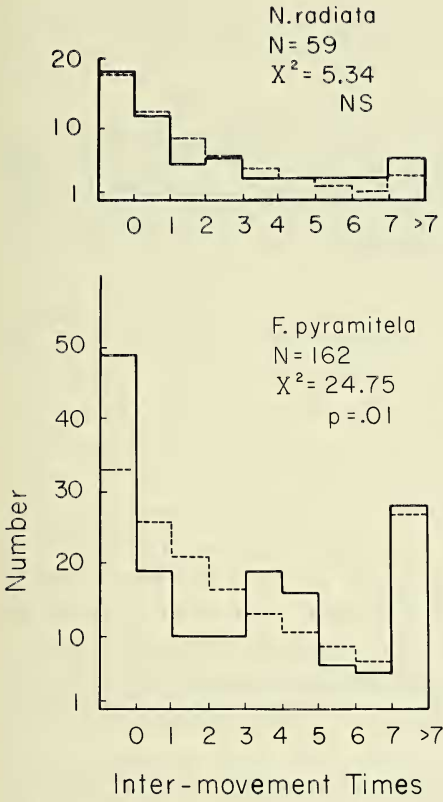
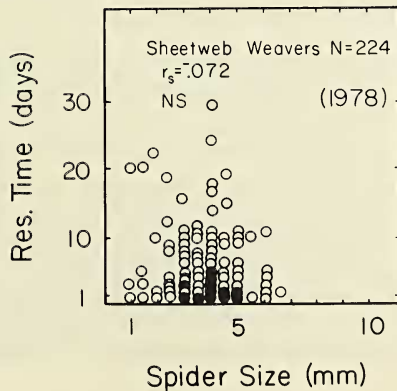
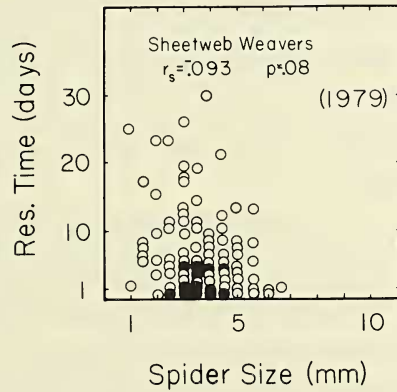


Fig. 5.—Distributions of residence times (inter-movement times) at websites. Solid lines: observed distributions. Dotted lines: expected distributions from hypothesis of randomly occurring movements.  $\chi^2$  and significance levels given on graphs.

Fig. 6.—Residence times at websites vs. body length of spider for sheetweb weaving guild (pooled data). Upper graph: 1978 field season. Lower graph: 1979 field season. Spearman rank correlation is shown. Black dots as before.



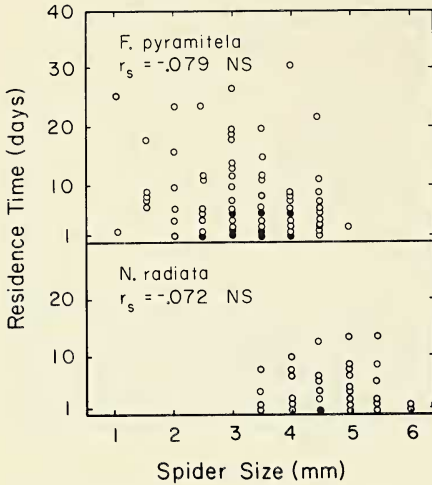


Fig. 7.—Residence times at web-sites vs. body length of spider for each species. Upper graph: *Frontinella pyramitela*. Lower graph: *Neriene radiata*. Spearman rank correlation is shown. Black dots as before.

The variation in body size also seems to have a negligible effect on the distributions of residence times at websites for the two species. There are slight differences between the two species in the average residence time at a website, but they are probably the result of differences in sample size rather than differences in biology. In both average residence time and fit to a random expectation, both species encompass nearly the entire range of variation seen in the guild as a whole; thus, the source of the variation for the guild is almost entirely intraspecific.

Wise (1975) has provided a set of field experiments bearing on the question of whether population growth of *N. radiata* is limited by the availability of food. He was able to show that adult female spiders lengthened their residence times at web-sites and increased their fecundity when their food supply was augmented. A negative effect of population density also existed such that the supply of food became a density-dependent factor.

In this study, orbweavers showed a tendency to stay at profitable websites and move quickly from sites not providing much food (Janetos 1982). Why did *F. pyramitela* and *N. radiata* not show the same trend, especially in light of Wise's (1975) study?

The answer probably lies in the different techniques used in the studies. Wise (1975) artificially enhanced food supplies at websites in order to test for food-limitation of individual fecundity and population growth rate. This study depended on the naturally occurring variation in food supply at undisturbed websites. The variation in numbers of prey captured per day and in the average size of prey at a website was less than that shown by orbweavers (Janetos 1982). Thus, the difference in results of the two studies reduces to the realization that Bowl and Doily Spiders and Filmy Dome Spiders are capable of adjusting their residence times at websites as a response to food supply, but that the variation in web site quality in my study was low enough that the behavior was not expressed. If all sites suitable for web-building are more or less equal in return rates of prey, there is little advantage in moving to a new website if the first few days at the present site are poor; a new site is unlikely to be better.

This does not necessarily mean that the linyphiids in this study were not food-limited. They may well have been. It does mean, however, that the behavioral tactic of leaving the current website in expectation of finding a "hot spot" was not adaptive, given the low variation in quality of websites. Thus, the distributions of residence times at

websites resemble those that would be expected from a hypothesis of random movements from sites, i.e. that there is a constant small probability of a stimulus to move occurring each day.

One further consequence of the relative uniformity in payoffs at websites is that there was no indication that competition for websites was important in this system. The second occupant of the site was not consistently larger than the first, as would be expected if aggressive interactions were common (Janetos 1982). In fact, in two field seasons, only one indisputable case of aggressive displacement was seen. This is in marked contrast to the case of *Agelenopsis aperta* (Riechert 1981). *A. aperta* lives in extremely harsh habitats (Riechert et al. 1973) and profitable websites in the habitat are in short supply (Riechert and Tracy 1975, Riechert 1974). Individuals battle over websites, with the larger spider usually winning (Riechert 1976, 1978). The major difference between the *A. aperta* system and this study is the number of suitable websites. The study site in New Jersey provided an abundance of possible websites. Since websites were not at a premium, one would not expect to see competitive interactions very often. The richness of the habitat makes such interactions unprofitable indeed.

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